# WORLD SPECIES OF THE WASP GENUS HOLOTACHYSPHEX DE BEAUMONT (HYMENOPTERA: SPHECIDAE)

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Abstract. – Species of Holotachysphex de Beaumont are revised for the first time. The revision includes a redescription of the genus, a key to the species, a phylogenetic analysis of species, a summary of the known life history, distribution records, and maps. Four species are recognized and redescribed using previously observed and newly discovered characters, but *Holotachysphex prosopigastroides* (Gussakovskij, 1952) remains a nomen dubium. Two new synonyms are established: *Holotachysphex turneri* var. *transvaalensis* (Arnold, 1924) = *turneri* (Arnold, 1923), and *pentapolitanus* (de Beaumont, 1960) = *mochii* (de Beaumont, 1947).

Key Words: Life history, phylogenetic analysis, redescription, distribution

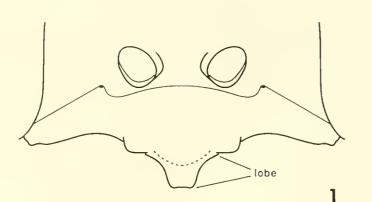
Holotachysphex is a small Old World genus of four or five species which was properly defined only recently. Specimens are rarely collected. Most species were originally described in Tachysphex, but de Beaumont (1940) established Holotachysphex (as a subgenus) to include holognathus Morice, 1897. Later Arnold (1951) proposed Phytosphex to include Tachysphex turneri Arnold, 1923, and Gussakovskij (1952) described Haplognatha for his new species prosopigastroides. Subsequently, de Beaumont (1955) synonymized Haplognatha with Holotachysphex, and Pulawski (1971) recognized Holotachysphex as a genus based on previously known and some newly-found characters; he included Phytosphex as a subgenus. Bohart and Menke (1976) redescribed Holotachysphex in detail but did not use subgenera because of the small number of the species, I share their opinion. The present paper is the first revision of the genus.

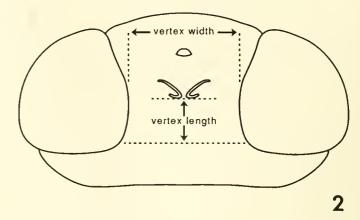
Technical terms.—Generally, I follow Bohart and Menke (1976) in their use of morphological terms, but Michener and Fraser's (1978) terminology is used for the mandible. A few terms not included in these publications are defined below and a few others need clarification or are redefined for convenience:

Clypeal lobe: the projecting anterior part of clypeus (Fig. 1).

Mandible (Figs. 13, 16):

- —adductor ridge: extends distad from the adductor swellings and gradually becomes visible from the outside (constituting the distal part of the mandibular posterior margin); the two portions differ in size, the distal one being higher than the basal one;
- -condylar ridge: arises from the condyle, extends distad, and forms the basal portion of the posterior mandibular margin; it is angulate distally in many Larrinae (including most *Gastrosericus*);
- -condyle: mandibular articulation on the occipital side of the head capsule;
- -notch: an emargination on the posterior





Figs. 1-2. Holotachysphex: 1-clypeus, 2-head in top view.

margin, delimited basally by the condylar ridge and distally by the expanded portion of the adductor ridge;

- posterior margin: extends between the condyle and mandibular apex; called externoventral margin by Bohart and Menke (1976) and lower margin by Michener and Fraser (1978); it actually consists of two components: the condylar ridge basally and the adductor ridge distally (the term *posterior* is preferred because the head is hypognathous, and this edge is thus oriented posterad);
- -trimmal carina (Figs. 13, 16): begins at some distance from the mandibular base and constitutes the inner mandibular margin (= cutting edge), except distally.

Sternum, tergum: shortened terms for gastral sternum, gastral tergum. Vertex (Fig. 2):

- —length: the distance between a hindocellus and an imaginary line connecting eye hindcorners (i.e. the point where the inner and the posterior portions of the orbit meet);
- -width: the shortest interocular distance in the ocellar region.

Sources of material.—Institutions that sent material for study or that are mentioned as type depositories are referred to in the text by the following abbreviations:

AMG Albany Museum, Grahamstown, South Africa (Friedrich W. Gess);

- BMNH British Museum (Natural History), London, England (Colin R. Vardy);
- CAS California Academy of Sciences, San Francisco, California, USA;
- MNHN Muséum National d'Histoire Naturelle, Paris, France (Janine Casewitz-Weulersse);
- MS Maximilian Schwarz, Ansfelden near Linz, Austria (personal collection);
- OXFORD Oxford University Museum, Hope Department of Entomology, Oxford, England (Christopher O'Toole);
- SAM South African Museum, Cape Town, South Africa (Vincent B. Whitehead);
- TMP Transvaal Museum, Pretoria, South Africa;
- USNM United States National Museum (= Smithsonian Institution), Washington, D.C., USA (Karl V. Krombein, Arnold S. Menke);
- ZIN Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

### Genus Holotachysphex

Holotachysphex de Beaumont, 1940:179 (as subgenus of *Tachysphex*). Type species: *Tachysphex holognathus* Morice, 1897, by monotypy.—Pulawski, 1971:10 (raised *Holotachysphex* to full generic status).

- Phytosphex Arnold, 1951:153. Type species: Tachysphex turneri Arnold, 1923, by original designation and monotypy. Pulawski, 1971:10 (as subgenus of Holotachysphex). Synonymized with Holotachysphex by Bohart and Menke, 1976: 44, 282.
- Haplognatha Gussakovskij, 1952:248. Type species: Haplognatha prosopigastroides Gussakovskij, 1952, by original designation and monotypy. Synonymized with Holotachysphex by de Beaumont, 1955: 222.

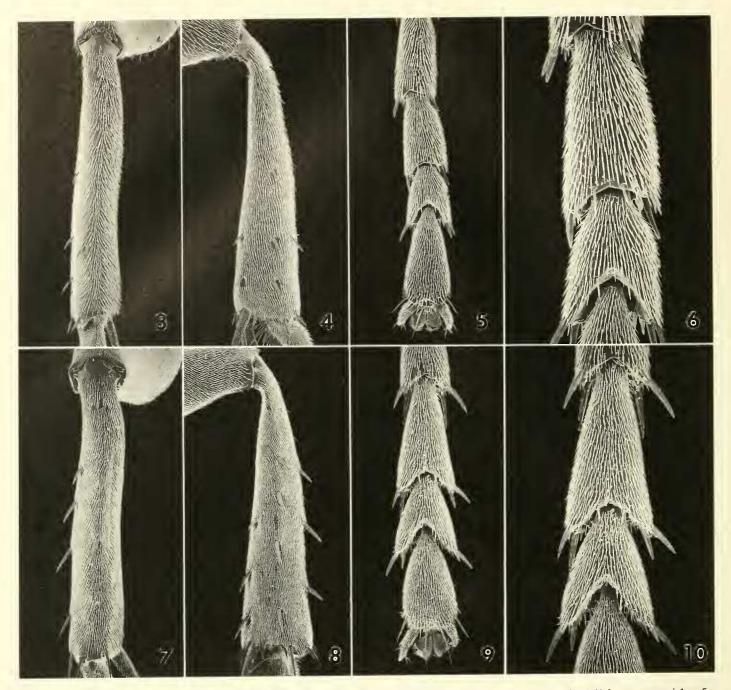
Diagnosis. - The flattened, elongate hindocellus is an apomorphy that places Holotachysphex in Larrini (Bohart and Menke, 1976). The following nine autapomorphies differentiate the genus from the other members of the tribe: 1. no foretarsal rake in either male or female (outer margin of forebasitarsus without preapical spines); 2. hindtibial dorsum with one or two, inconspicuous, nearly appressed bristles instead of spines (Figs. 3, 4); 3. no pygidial plate in female (plate indicated only apically by two vestigial structures, a slightly inflected integument and a row of setigerous punctures); 4. clypeal lobe pointed (sharply or roundly), not angulate laterally but flanked by small tooth or oblique carina adjacent to free margin (Figs. 1, 17, 24, 26), although tooth and carina are evanescent in some specimens: 5. male hindtarsomeres II-IV almost parallel-sided except basally (Figs. 5, 6); 6. tergum II carinate laterally (the carina is barely visible in Fig. 11); 7. male sterna II and III or II-IV with large patches of velvety pubescence (Figs. 11, 12); 8. nests established in hollow twigs; and 9. pyrgomorphid Acridoidea used as prey (but see number 9 in next paragraph).

For comparison, the character states found in other Larrinae are: 1. foretarsal rake present at least in the female (except absent in *Paraliris*), forebasitarsus with at least three rake spines; 2. hindtibial dorsum with one to several suberect spines (Figs. 7, 8); 3.

pygidial plate well defined except rudimentary in Tachysphex erythropus (Spinola), mendozanus Brèthes, and nepharius Pulawski: 4. clypeus either not pointed or, when pointed, with no lateral tubercle or carina; 5. male hindtarsomeres II-IV broadening evenly toward apex (Figs. 9, 10), with a few exceptions such as the strongly expanded hindtarsomere II of Liris haemorrhoidalis Fabricius: 6. tergum II not carinate laterally in most genera, but carina present in most Prosopigastra (rudimentary or absent in creon (Nurse) and nubigera Gussakovskij). a weak, longitudinal carina also present in some large Australian Tachysphex, especially females (e.g. hypoleius F. Smith, persistans R. Turner, pugnator R. Turner, and stimulator R. Turner); 7. male sterna without specialized areas except sterna III and IV with fimbriate or setal patches in several Gastrosericus; 8. nesting takes place in the ground (unknown in *Paraliris*); and 9. prey other than Pyrgomorphidae: mostly various other orthopteroids, but also lepidopterous larvae (some Tachytes, some Parapiagetia), Heteroptera (Prosopigastra), teneral asilids (Gastrosericus asilivorus Pulawski), and cicadellids (Gastrosericus chalcithorax Arnold); this information may be insufficient: many Pyrogomorphidae greatly resemble Acrididae, a common prey of Tachysphex and Tachytes, and are perhaps used as well.

Description.—*Holotachysphex* was described in detail by Bohart and Menke (1976), but is redescribed here to include characters not used by them. Major structural characters, other than the apomorphies discussed in the Diagnosis, are the following.

Mandible: posterior margin emarginate in some species (Fig. 16), entire in others (Fig. 25); trimmal carina without cleft but with prominent tooth (Fig. 13); distal portion of adductor ridge not expanded, straight or weakly convex (roundly expanded in *Tachysphex*). Frons without swellings or carinae, but with oblong glabrous tubercle

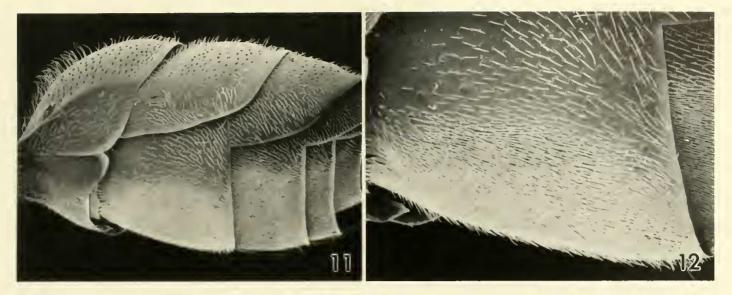


Figs. 3-6. Holotachysphex holognathus: 3-female hindtibia dorsally, 4-female hindtibia, outer side, 5-male hindtarsomere II-V, 6-male hindtarsomere III-IV.

Figs. 7-10. Tachysphex pompiliformis (Panzer): 7-female hindtibia dorsally, 8-female hindtibia, outer side, 9-male hindtarsomere II-V, 10-male hindtarsomere III-IV.

above each antennal socket (tubercles convergent above). Hindocellar scars diverging anterolaterad (Fig. 2), moderately elongate (scar shorter than distance that separates it from midocellus). Occipital carina joining hypostomal carina. Propodeum short, distance betwen metanotum and spiracle less than spiracle's length; dorsum setose throughout. No additional sclerites between metasternal apex and propodeum. Third submarginal cell present, not petiolate. Forecoxal apex not expanded into apical process. Foretarsomere I with three or four ventral spines in female and one in male (length of spines no more than tarsomere apical width). Hindtarsomere II  $0.6-0.7 \times$ length of hindtarsomere I. Gastral punctures conspicuous. Tergum I without short, oblique carina extending from anterolateral corner, tergum II carinate laterally. Female: tarsal claws without tooth; tergum VI fairly convex, markedly more so than in *Prosopigastra*; sting including sheaths circular in cross section. Male: tergum VII not depressed apically.

Additional characters that vary in related



Figs. 11-12. Holotachysphex holognathus: 11-male gaster obliquely, 12-male sternum II obliquely.

genera but which are universal in Holotachysphex include the following. Labrum flat, narrow (markedly more so than in Tachysphex), emarginate apically; stipes flat. Mouthparts not elongate. Paramandibular process broadly separated from back side of clypeus (mandibular socket open). Clypeus produced into a mesal lobe. Inner orbits convergent above. Vertex broad, width at least  $1.5 \times$  length (not clearly species-specific). Mesothoracic punctures coarse, mesopleural punctures less than one diameter apart (most specimens) or several punctures about one diameter apart (some turneri). Episternal sulcus incomplete (ending near anteroventral mesothoracic margin). Propodeal dorsum and hindface rugose, side coarsely, irregularly ridged (ridges evanescent anteriorly). Marginal cell long (foremargin  $3.4-3.9 \times$  maximum width). Hindcoxa: inner dorsal carina not expanded basally. Foretibia without spines on outer side. Hindtibia not ridged. Female: forefemoral venter with minute punctures; outer side of foretibia without spines; apicoventral margin of tarsomere IV shallowly concave; and apicoventral margin of tarsomere V straight. Male: forecoxa and foretrochanter unmodified; forefemur emarginate basally; tergum VII with evanescent lateral carina; sternum VIII emarginate apically. Setae erect or nearly so adjacent to hypostomal carine.

Relationships to other Larrini. - In their dendrogram of larrin genera, Bohart and Menke (1976) indicated that Holotachysphex was a sister group of Tachysphex + Parapiagetia and that Prosopigastra and Kohliella were closely related. The dendrogram was presumably based on 50 larrin characters listed on page 224. However, branches were not supported by character distribution, and plesiomorphic character states may have been used as well. Pulawski (1979) recognized additional apomorphies and analyzed phylogenetic relationships of Holotachysphex and the latter three genera. My current analysis indicates that Holotachysphex belongs to a holophyletic lineage that also includes Kohliella, Parapiagetia, and Tachysphex (but not Prosopigastra) and which is characterized by a unique synapomorphy: an oblong, glabrous swelling above each antennal socket. In addition, all four genera lack a basal oblique carina on tergum

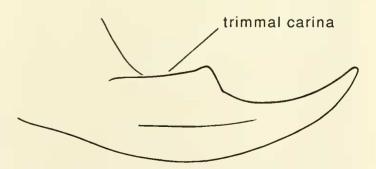


Fig. 13. *Holotachysphex turneri*: mandible, anterior face.

I, an apomorphy also shared with Gastrosericus. The carina is also absent in many Tachytes and one Larropsis (chilopsidis Cockerell and W. Fox), apparently a parallelism, but present in the remaining Larrinae and also in most other Sphecidae (species with petiolate gaster such as Sphecinae and most Pemphredoninae are obvious exceptions). Within the lineage, Holotachysphex is most closely related to Tachysphex, sharing two apomorphies with the latter (Pulawski 1979): sting, including sheaths, circular in cross section and male forefemur emarginate (the entire forefemur of several specialized Tachysphex is clearly a reversal). Holotachysphex has nine autapomorphies (see Diagnosis), but Tachysphex appears to be paraphyletic; at least no autapomorphies have been found so far. Most probably, Holotachysphex was derived from a *Tachysphex*-like ancestor by switching from ground-nesting to twig-nesting, with subsequent loss of structures no longer used in digging: the foretarsal rake, hindtibial spines, and pygidial plate. Four other apomorphies have no known function (a sharply-pointed clypeus, parallel-sided male hindtarsomeres, lateral carina of tergum II, and velvety patches on male sterna).

Character analysis.—Eight characters were analyzed, of which the first seven have been polarized and one remains unpolarized. The polarized characters are (0: plesiomorphic, 1: apomorphic):

1. Posterior mandibular margin: 0. stepped (notched), 1. straight (entire).

An entire mandible is clearly plesiomorphic within the Sphecidae as a whole, and the notched mandible of most Larrinae is clearly derived (Menke 1988). In taxa with a primarily entire mandible (e.g. Pompilidae, *Sphex, Chlorion*), the adductor ridge is a single, continuous structure, gradually increasing in size toward the apex but not differentiated. This is the plesiomorphic condition. In Larrinae with emarginate mandibles, the ridge is differentiated into proximal and distal portions, separated from each other by an angle, a gap, or a slight overlap. This is the apomorphic condition. In *Holotachysphex*, the two portions are clearly differentiated, with a small overlap between them (the overlap area is shiny and difficult to see), indicating that the entire mandible of some species is a reversal rather than the primitive state. In *Holotachysphex*, the mandible is notched in *sacalava* and *turneri*, and entire in *holognathus* and *mochii*.

2. Apical emargination of male sternum VIII: 0. broad shallow, 1. narrow, deep.

Male sternum VIII is broadly, shallowly emarginate in *Tachysphex* and most *Holotachysphex* (e.g. Figs. 18, 27), but narrowly, deeply emarginate in *Holotachysphex holognathus* (Fig. 31).

3. Volsellar setae: 0. of equal length, 1. short or absent mesally.

The former condition is found in *Tachy-sphex* and *Holotachysphex sacalava* and *turneri*, the latter in *Holotachysphex holog-nathus* and *mochii*.

4. Forefemoral notch of male: 0. bottom flat, with low carina, 1. bottom compressed into a conspicuous, longitudinal carina.

The notch bottom is flat in the vast majority of *Tachysphex*, but it is compressed into a crest in a few species such as *apricus* Pulawski and *erythropus* Spinola, specialized members of their respective lineages. It is also flat in *Holotachysphex holognathus*, but compressed in the other three species.

5. Hindtibial dorsum: 0. setose throughout, 1. glabrous.

The hindtibial dorsum is setose throughout in *Tachysphex* and *Holotachysphex* except narrowly glabrous in *Holotachysphex turneri*.

6. Tergal punctures: 0. fine or medium size, 1. coarse.

Tergal punctures of *Holotachysphex holognathus* are coarser than in other species of the genus and in *Tachysphex*.

7. Tergal setae: 0. all setae short, 1. basal setae of tergum I long.

Tergal setae are short in *Tachysphex* except basal setae of tergum I are long in *al*-

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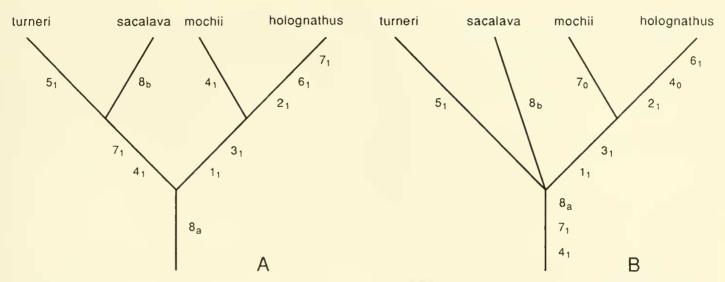


Fig. 14. Phylogenetic relationships among species of *Holotachysphex*. Numbers represent apomorphic character states discussed on page 228. Numerical subscripts indicate the originally polarized characters, and the alphabetical subscript the originally unpolarized character. 1-posterior mandibular margin entire, 2-male sternum VIII deeply emarginate, 3-volsellar setae shortened or absent mesally, 4-forefemoral notch with compressed bottom, 5-hindtibial dorsum glabrous, 6-tergal punctures coarse, 7-setae of tergum I elongate basally, 8-clypeal lobe pointed or rounded (A), clypeal lobe truncate (B).

bocinctus (Lucas), laticauda Gussakovskij, maculipennis Pulawski, nubilipennis de Beaumont, pilosulus R. Turner, and priesneri de Beaumont. These species (except priesneri) are the most specialized within the genus (Pulawski 1971), thus their long tergal setae are apparently apomorphic. The setae are short in Holotachysphex mochii and long in the other three.

I was unable to polarize the following character:

8. Clypeal lobe: a. sharply pointed or rounded apically, b. truncate apically.

The lobe is truncate in *Holotachysphex* sacalava and pointed or rounded in the other three species. A variety of shapes is found in *Tachysphex* and other Larrini in general.

Phylogenetic analysis. – Of the eight binary characters considered, four were synapomorphies (1, 3, 4, 7), three were autapomorphies (2, 5, and 6), and one was unpolarized (8). Two equally parsimonious cladograms of 10 steps each (Fig. 14A, B) were generated using Hennig86 version 1.5, a parsimony computer package by James F. Farris. One is fully resolved and symmetrical, the other is unresolved, and the consistency index (for characters other than autapomorphies) is 0.71. Both trees suggest that the two species of the Northern Hemisphere, *holognathus* and *mochii*, are sister species (thus closer to each other than either to *sacalava* or *turneri*) and that the apically truncate clypeal lobe of *sacalava* is derived. The resolved tree (Fig. 14A) suggests that:

1. Holotachysphex sacalava and turneri also are sister species.

2. The compressed femoral notch was convergently acquired twice: by the common ancestor of *sacalava* + *turneri* and by *mochii*.

The unresolved cladogram (Fig. 14B), which requires no convergence, suggests that:

1. *Holotachysphex sacalava* and *turneri* originated independently from the common ancestor of the genus.

2. The originally noncompressed femoral notch (4) evolved into a carinate notch in *Holotachysphex* and then reverted to noncompressed in *holognathus*; similarly, the originally short tergal setae first evolved into long and then reverted into short in *mochii*.

I see no reason to prefer one interpretation over the other.

Life history.—Studied only in *Holotachy*sphex turneri (see this species for details and references). Nests are made in hollow stems, and nymphs of pyrgomorphid grasshoppers (Acridoidea) are used as prey. The lack of a foretarsal rake and a pygidial plate in the female suggests that other species also nidify in stems rather than in the ground.

Geographic distribution (Fig. 15).—Africa, Greece (only Peloponnesus), Turkey and adjacent Mediterranean islands (Crete, Cyprus, Rhodes), Israel, Arabian Peninsula, Iran, Tajikistan, India, and Sri Lanka. Ranges of individual species overlap in Ghana and Kenya (*holognathus* and *turneri*) and in the eastern Mediterranean region (*holognathus* and *mochii*).

# Key to the Species

1.	Mandibular posterior margin notched (Fig. 16).
-	Mandibular posterior margin entire (Fig. 25).
2.	Clypeal lobe sharply pointed (Fig. 17); tibiae red to brown; hindtibial dorsum narrowly gla- brous (Fig. 20); Subsaharan Africa
-	Clypeal lobe truncate apically (Fig. 24); tibiae partly or all black; hindtibia setose throughout; Madagascar
3.	
_	Clypeus different (Figs. 26, 30) 4
4.	Setae straight on vertex, appressed on tergum I, setal length about one midocellar diameter; free margin of clypeal lobe convex basally and concave distally; male sternum VIII shallowly, broadly emarginate (Fig. 27); Libya to Iran.
-	Setae sinuous on vertex, erect on tergum I, setal length markedly more than one midocellar di- ameter; free margin of clypeal lobe evenly con- cave (Fig. 30); male tergum VIII deeply emar- ginate apically (Fig. 31); Africa north of Equator to Sri Lanka holognathus (Morice)

## DESCRIPTIONS OF SPECIES

## Holotachysphex turneri Arnold (Figs. 16–23)

Tachysphex Turneri Arnold, 1923:165, 9, 8 (as Brauns's manuscript name), incorrect original capitalization. Holotype: sex not indicated, South Africa: Cape Province: Willowmore (SAM). – In *Phytosphex*: Arnold, 1951:153 (new combination, type species of *Phytosphex*), 154 (Ethiopia). – In *Holotachysphex*: Bohart and Menke, 1976:282 (new combination, listed); Gess, 1978:209 (nest, prey); Gess and Gess, 1980:52 (nest); Gess, 1981:30 (South Africa), 34, 66, 68, and 69 (nesting).

Tachysphex Turneri var. transvaalensis Arnold, 1924:66, 9. Holotype: 9, South Africa: Transvaal: Lichtenburg (TMP). New synonym.—As Holotachysphex turneri transvaalensis: Bohart and Menke, 1976: 282 (new combination, listed).

Diagnosis.—*Holotachysphex turneri* differs from other species by the combination of a notched mandible and a sharply pointed clypeal lobe (Fig. 17), and the narrowly glabrous hindtibial dorsum is also distinctive. The tibiae are all red (brown in some specimens), a subsidiary recognition feature.

Description.—Mandible (Fig. 16): posterior margin notched (condylar ridge acutely expanded apically, distal portion of adductor ridge convex). Clypeal lobe sharply pointed, its free margin evenly concave on each side of apex (Fig. 17). Punctures of terga I and II somewhat larger than those adjacent to hypostomal carina.

Setae partly sinuous on head and thorax, erect and markedly longer than midocellar diameter on vertex and tergum I. Hindtibial dorsum narrowly glabrous dorsally (Fig. 20).

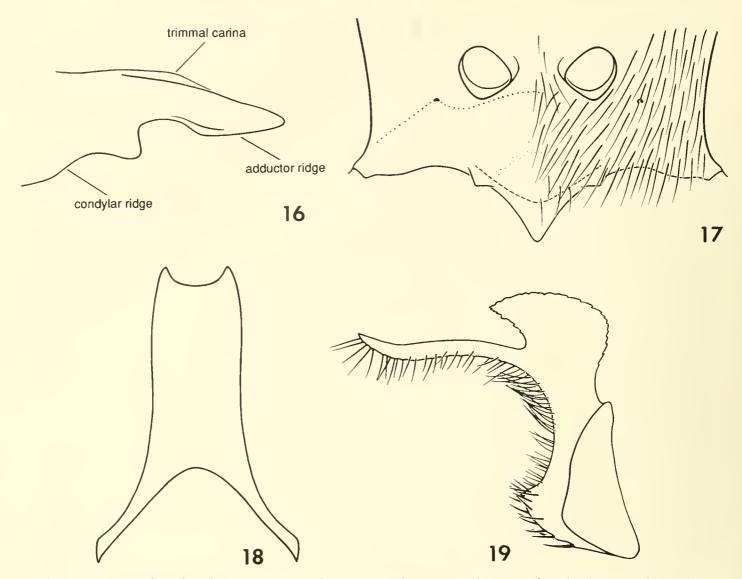
Gaster varying from all red to all black (see Variation below for details). Femora black except red apically in most specimens. Tibiae and tarsi either red (most specimens) or brown (one male from Hilton).

Female. – Dorsal length of flagellomere I 1.8–1.9× apical width. Vertex width 1.9– 2.3× length. Length 7.0–9.5 mm.

Male.—Dorsal length of flagellomere I  $1.9 \times$  apical width. Vertex width  $2.3-2.5 \times$ width. Bottom of forefemoral notch asetose, compressed into well-defined, longitudinal crest (Figs. 21, 22). Sternum VIII shallowly,



Fig. 15. Overall geographic distribution of the genus Holotachysphex (shadowed area).

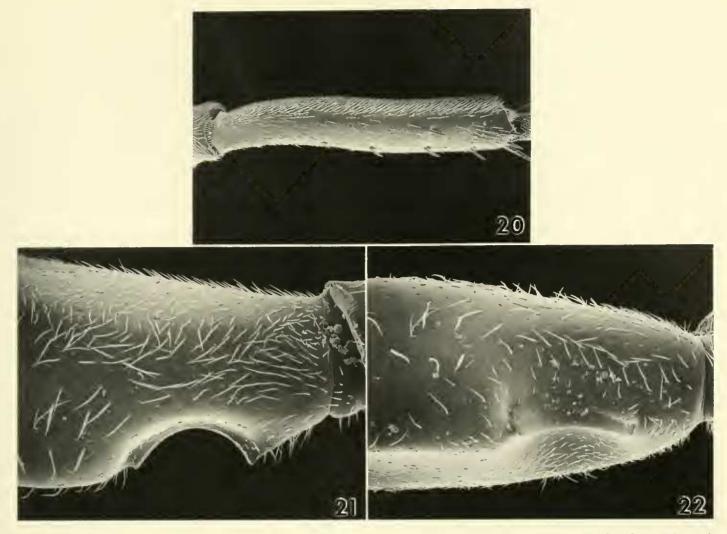


Figs. 16–19. *Holotachysphex turneri*: 16–female mandible, outer side, 17–female clypeus, 18–male sternum VIII, 19–volsella.

roundly emarginate apically (Fig. 18), slightly less so than in *holognathus*. Length 6.0–7.5 mm. Gonostyle ventrally with numerous setae that become shorter toward gonostyle apex. Volsella (Fig. 19): ventral margin setose from base to apex.

Color variation and recognition of subspecies.—Gastral color of *turneri* varies both geographically and individually. Generally, the further south from the equator the darker the specimens: the gaster is all red in Ghanaian and Kenyan specimens, but tergum I is black basally in those from Zambia, Zimbabwe, and Transvaal; and the black covers base of tergum I as well as tergum III and the following terga in most specimens from Cape Province and also in some from Zimbabwe (two such males from Bubi Valley have been examined). Individual variation occurs in specimens from Bubi Valley (Zimbabwe) as well as Willowmore and Hilton (Cape Province). In the first locality, the male gaster is either all red (except the basal spot) or partly black as described above. In males from Willowmore, tergum II is either all red or largely black (except red basomedially and laterally). In the females from Hilton, tergum III is either black or reddish; and in the males, the gaster is either all black or partly red (the red covering tergum I posteriorly, tergum II, and sternum II). One of these color forms, the one from Transvaal, was named var. transvaalensis by Arnold (1924) and then raised to the subspecies rank by Bohart and Menke (1976). In my opinion, color forms of turneri do not warrant formal names as they are mostly clinal and not clearly delimited. Consequently, I re-

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Figs. 20–22. *Holotachysphex turneri*: 20 – female hindtibia with asetose dorsum, 21 – male forefemoral notch in profile, 22 – same, bottom view.

gard *transvaalensis* as a junior synonym of this species

Life history. - Arnold (1923) first noticed the unusual nesting habits of turneri, which were subsequently studied in detail by Gess (1978). Nests are a linear series of cells founded in hollow stems, e.g. of Aloe and Datura (Arnold 1923), or abandoned galleries of Xylocopa caffrariae Enderlein in internodes of Phragmites australis (Cav.) Steud. (Gess and Gess 1980). The stems used can be lying on the ground or up to 2 m above. A terminal plug of clay or detritus is constructed at the bottom of the gallery, and individual cells are separated by similar plugs (intercellular plugs consist of detritus on the inner side and earth on the outer side). Small nymphs of a short-horned grasshopper, probably Pyrgomorpha or Pyrgomorphella (Pyrgomorphidae, Acridoidea), are used as prey. They are stored head in and not completely paralyzed. The number of prey per cell (4–32) is inversely proportional to their size (length 3.2–12.0 mm). The wasp's egg or later the larva is positioned across the prey's body, with the mouth end just behind the prothoracic coxa.

Geographic distribution (Fig. 23).—Ghana and Ethiopia to southern South Africa.

Records. – ETHIOPIA: Addis Ababa (Arnold 1951).

GHANA: Kawampe, 8°30'N, 1°35'W, 45 km N Kintampo (4 *d*, CAS).

KENYA: Archer's Post on Ewaso Ngiro River (1 9, 1  $\delta$ , CAS).

SOUTH AFRICA: Cape Province: Hilton 18 km WNW Grahamstown (1 9, CAS; 8 9, 4 8, AMG), Willowmore (1 9, 1 8, BMNH; 1 9, 2 8, SAM). Transvaal: Lichtenburg (Arnold 1924).

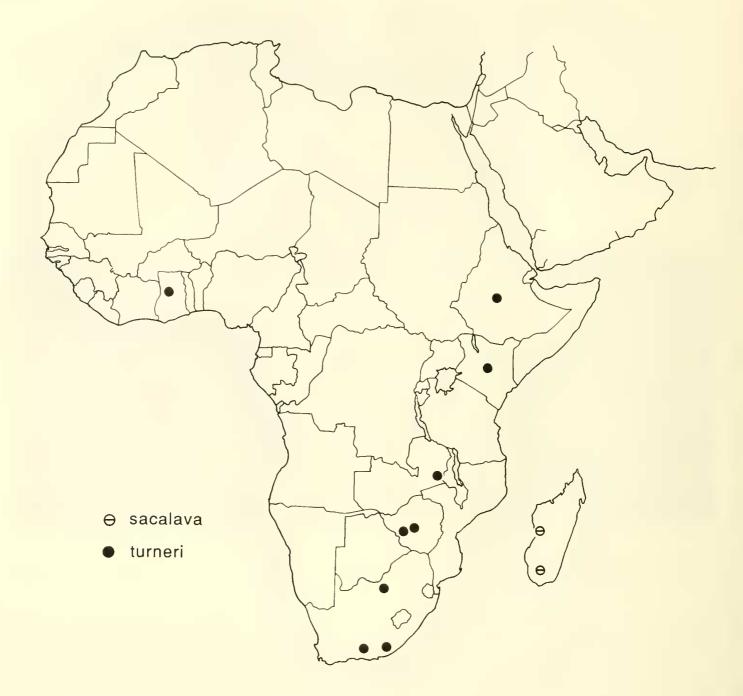


Fig. 23. Geographic distribution of Holotachysphex sacalava and turneri.

ZAMBIA: Mid Luangwa Valley (2 9, BMNH).

ZIMBABWE: Bubi Valley (3 &, SAM), Bulawayo (1 ?), Hillside (1 ?, BMNH), Nyamandhlovu (1 ?, BMNH), Redbank (1 ?, SAM), Rhodesdale Ranch (Arnold 1924).

# Holotachysphex sacalava Arnold (Figs. 23, 24)

Tachysphex Turneri sacalava Arnold, 1945: 106, ♀, ♂. Lectotype: ♀, Madagascar: Bekily (MNHN), present designation.—As Holotachysphex sacalava: Menke in Bohart and Menke, 1976:282 (new status, new combination, listed).

Diagnosis.—*Holotachysphex sacalava*, known only from Madagascar, has a unique clypeus: the lobe is truncate apically, and the free margin is evenly concave on each side of the truncation (Fig. 24). The all red gaster is also diagnostic in combination with partly black tibiae.

Description.-Mandible: posterior margin notched (condylar ridge acutely expand-

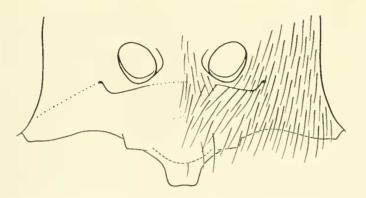


Fig. 24. Holotachysphex sacalava: female clypeus.

ed apically, distal portion of adductor ridge convex). Clypeal lobe pointed, truncate apically, free margin evenly concave on each side of apex (Fig. 24). Punctures of terga I and II about as large as those adjacent to hypostomal carina.

Setae of vertex and tergum I erect, sinuous, markedly longer than midocellar diameter. Hindtibia setose throughout.

Gaster red. Femora black; tibiae and tarsi partly brown or reddish, remainder black.

Female. – Dorsal length of flagellomere I  $1.9-2.2 \times$  apical width. Vertex width 1.7– $1.9 \times$  length. Length 8.0–11.0 mm.

Male. – Dorsal length of flagellomere I 1.9× apical width. Vertex width  $1.8 \times$ length. Bottom of forefemoral notch asetose, compressed longitudinally into sharp crest, as in *turneri* (see Figs. 21, 22). Sternum VIII roundly emarginate apically, as in *turneri* (see Fig. 18). Length 7.3–9.0 mm. Gonostyle ventrally with numerous setae that become shorter toward gonostyle apex. Volsella as in *turneri* (see Fig. 19).

Geographic distribution (Fig. 23). – Madagascar.

Records. – MADAGASCAR: Bekily (1 9, 1 8, BMNH; 1 9, CAS; 10 9, 2 8, including lectotype and paralectotype of *sacalava*, MNHN; 1 9, USNM), Bereboka 60 km NE Morondava (1 9, 1 8, BMNH; 1 9, CAS).

## Holotachysphex mochii de Beaumont (Figs. 25–29)

Tachysphex mochii de Beaumont, 1947b: 676, 9. Holotype: 9, Greece: Rhodes Island: no specific locality (A. Mochi collection, Rome), examined by Pulawski, 1972:818.—In *Holotachysphex*: Pulawski, 1972:818 (new combination, taxonomy); de Beaumont, Bytinski-Salz and Pulawski 1973:13 (recorded from Israel); Bohart and Menke, 1976:282 (listed).

- Tachysphex pentapolitanus de Beaumont, 1960:241, 9. Holotype: 9, Libya: Cyrenaica: Barce, now Al Marj (BMNH), examined. New synonymy. — In *Holotachysphex*: Bohart and Menke, 1976:282 (new combination, listed).
- Tachysphex schwarzi Pulawski, 1967:408, 9, 8. Holotype: 8, Turkey: Mersin Province: Mut (M. Schwarz collection, Linz), reexamined in 1989. Synonymized with Holotachysphex mochii by Pulawski, 1972:818.

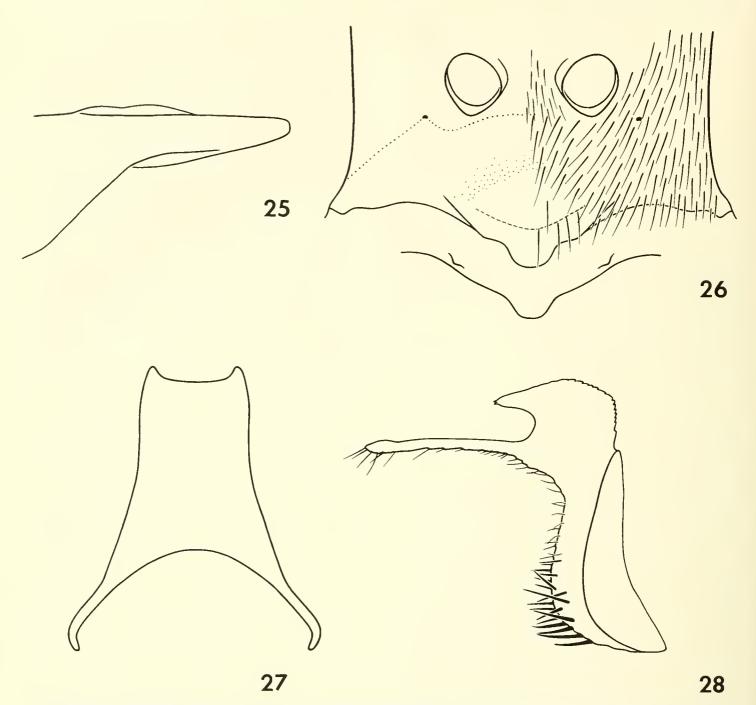
Diagnosis.—*Holotachysphex mochii* is unique in having the following: the setae are straight, short on vertex (about one midocellar diameter long) and appressed on tergum I; and male sternum VIII is broadly, shallowly emarginate (Fig. 27). In all other *Holotachysphex*, the setae, on both vertex and tergum I, are sinuous, erect, and markedly longer than one midocellar diameter; and male sternum VIII is roundly emarginate (compare Figs. 18, 31).

Description.—Mandible (Fig. 25): posterior margin gently curved (condylar ridge not expanded apically, distal portion of adductor ridge straight). Clypeal lobe rounded apically, free margin convex basally and concave apically on each side of apex (Fig. 26). Tergal punctures finer than in other species, about as large as those adjacent to hypostomal carina.

Setae straight, appressed or nearly so; setal length about 1.3–1.5 midocellar diameter on vertex, about 1.0 midocellar diameter on tergum I. Hindtibia setose throughout.

Female. – Dorsal length of flagellomere I  $1.7 \times$  apical width. Vertex width  $1.5-1.6 \times$  length. Length 9.0–10.0 mm.

Gaster nearly all black (sternum II red) to largely red (terga III and V mesally and



Figs. 25–28. *Holotachysphex mochii*: 25–female mandible, outer side, 26–female clypeus, 27–male sternum VIII, 28–volsella.

tergum IV except laterally black). Legs black (Libyan specimen) or femora, tibiae, and tarsi red (femora black basally in some specimens).

Male. – Dorsal length of flagellomere I  $1.5-1.6 \times$  apical width. Vertex width 1.6– $1.8 \times$  length. Bottom of forefemoral notch asetose, compressed into sharp, longitudinal crest, as in *turneri* (see Figs. 21, 22). Sternum VIII: apical margin shallowly, broadly concave (Fig. 27). Length 6.0–8.8 mm. Gonostyle ventrally with only a few, short, inconspicuous setae. Volsella (Fig. 28): setae of ventral margin shortened mesally.

Gaster black or tergum I brown reddish mesally. Femora black (except apically), tibiae black (Iranian male) or reddish dorsally and dark brown ventrally.

Geographic distribution (Fig. 29). – Turkey and adjacent Mediterranean islands (Rhodes, Cyprus), Israel, Iran, also Libya (Cyrenaica).

Records.—CYPRUS (Pulawski 1972): Polemidia Hills, Yermasoyia River. GREECE: Rhodes Island: Ixia (Pulawski 1972).

ISRAEL: Tiberias (1 &, CAS).

IRAN: Khorasan: Fathabad 38 km NW Mashad (1 &, CAS).

LIBYA: Cyrenaica: Barce, now Al Marj (1 9, BMNH).

TURKEY: Mersin: Mut (3 å, CAS; 1 ¢, 2 å, MS). Urfa: Birecik (1 ¢, CAS).

## Holotachysphex holognathus Morice (Figs. 29–35)

- *Tachysphex* (?) *integer* Morice, 1897:308, 9, 8. Lectotype: 8, Egypt: Zeitun in Cairo area (OXFORD), present designation. Nec *Tachysphex integer* Kohl, 1892 = *Parapiagetia genicularis* (F. Morawitz, 1890).
- Tachysphex holognathus Morice, 1897:434, new name for Tachysphex integer Morice.-de Beaumont, 1940:179 (revision, recorded from Egypt), 1947a:212 (revision, recorded from Egypt), 1961:50 (recorded from Crete Island), 1965:53 (recorded from Crete Island). – In Holotachysphex: Pulawski, 1972:818 (new combination, taxonomy); de Beaumont, Bytinski-Salz and Pulawski, 1973:13 (recorded from Israel); Bohart and Menke, 1976 (listed); Krombein, 1980:123 (Sri Lanka).
- Tachysphex pollux Nurse, 1903:516, δ, examined by Pulawski, 1975:312. Holotype: δ, India: Gujarat: Deesa (BMNH). Synonymized with Holotachysphex holognathus by Pulawski, 1975:313.
- *Tachysphex* sp.: de Beaumont, 1961:50 (Crete Island).

Diagnosis.—*Holotachysphex holognathus* can be recognized by combination: posterior mandibular margin entire and setae of tergum I erect. Also, punctation of terga I and II is coarser than in other *Holotachysphex* (punctures larger than those adjacent to hypostomal carina). In the male, the forefemoral notch is flat, not compressed into a longitudinal crest (compressed in the other species).

Description. – Mandible: posterior margin straight (condylar ridge not expanded apically, distal portion of adductor ridge straight). Clypeal lobe roundly pointed, with free margin evenly concave on each side of apex (Fig. 30). Tergal punctures coarser than in other *Holotachysphex*, punctures of terga I and II conspicuously larger than those adjacent to hypostomal carina.

Setae partly sinuous on head and thorax; on vertex and tergum I erect, markedly longer than midocellar diameter. Hindtibia setose throughout.

Gaster black. Tibiae and tarsi black (most specimens), brown (female from Kerdasa, males from Crete), or red (male from Kenya).

Female. – Dorsal length of flagellomere I 1.8–2.0× apical width. Vertex width 1.5– 1.8× length. Legs black. Length 8.5–11.5 mm.

Male. – Dorsal length of flagellomere I 1.7–1.8× apical width. Vertex width 1.7– 1.8× length. Sternum VIII roundly emarginate apically (Fig. 31), emargination somewhat deeper than in *turneri*. Bottom of forefemoral notch setose, broad, with low, longitudinal ridge but not compressed into crest (Figs. 33–35). Length 7.5–8.5 mm. Gonostyle ventrally with only a few, short, inconspicuous setae. Volsella (Fig. 32): ventral margin setose only basally.

Geographic distribution (Fig. 29).—Senegal to Kenya to Egypt, Greece (Crete Island and Peloponnesus), Israel and Arabian Peninsula to India and Sri Lanka.

Records. – EGYPT: Cairo area: Cairo (1 9, 1 å, BMNH; 1 9, OXFORD), Ghiza (1 9, CAS), Kerdasa (1 9, USNM), Koubba (1 9, OXFORD), Zeitun (1 å, OXFORD, lectotype of *integer* Morice).

GHANA: Kawampe 45 km N Kintampo, 8°30'N, 1°35'W (1 9, 2 8, CAS), Legon 12 km NNE Accra (4 9, 1 8, CAS).

GREECE: Crete Island: Gortis and He-

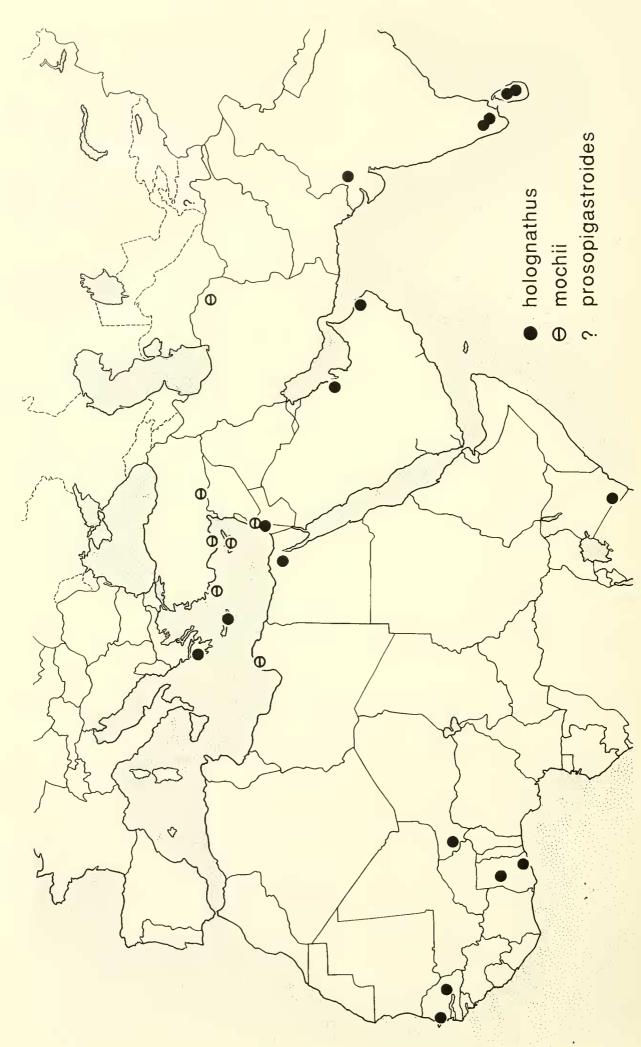
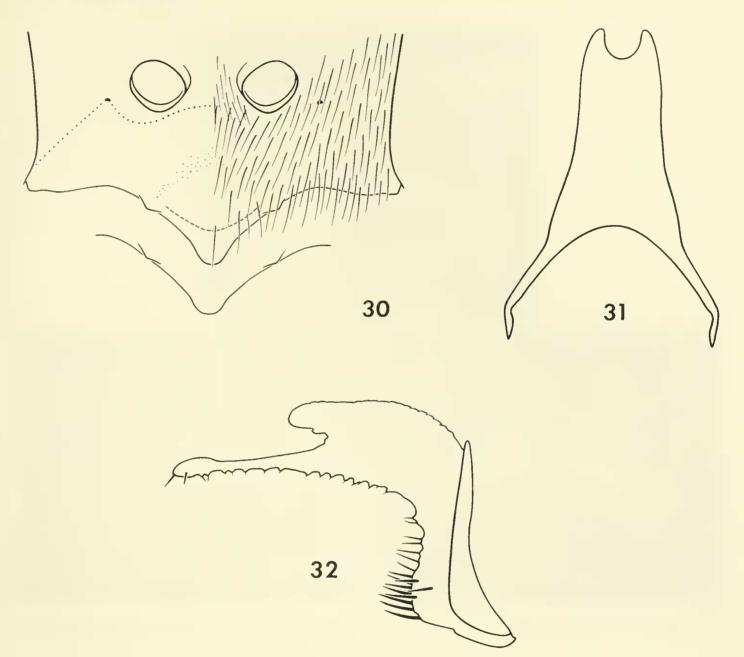


Fig. 29. Geographic distribution of Holotachysphex mochii, holognathus, and prosopigastroides.

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Figs. 30–32. Holotachysphex holognathus: 30-female clypeus, 31-male sternum VIII, 32-volsella.

raklion (de Beaumont, 1961), Knossos (1 ð, CAS), Yortys (1 ð, CAS). Ilia (in Peloponnesus): mouth of Alfios River (1 ð, BMNH).

INDIA: Gujarat: Deesa (1 ô, BMNH, holotype of *Tachysphex pollux*). Tamil Nadu: Alagar Kovil in Madurai District (1 ô, BMNH), Coimbatore (1 9, USNM).

ISRAEL: Jericho (de Beaumont, Bytinski-Salz and Pulawski 1973).

KENYA: Kitani Lodge in Tsavo National Park (1 &, CAS).

NIGER: Say (1 &, BMNH).

OMAN: Rostaq (1 9, 1 8, BMNH).

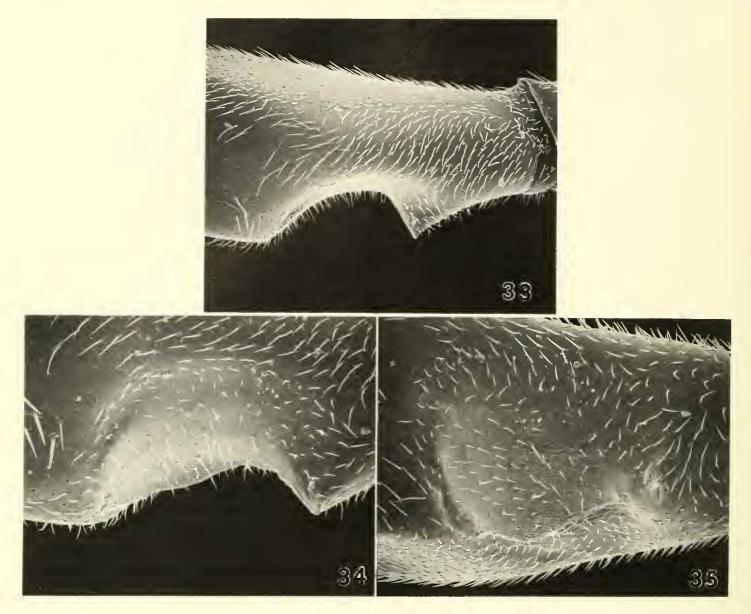
SAUDI ARABIA: Hofuf (1 º, 1 ð, BMNH).

SENEGAL: Tambacounda (1 º, CAS), 5 km SW Thiès (2 º, 3 ð, CAS).

SRI LANKA: Anuradhapura: Amarivayal (2 º, CAS, USNM), Hunuwilagama (1 º, USNM), Padaviya (2 º, USNM). Kandy: 5 mi NW Mahiyangana (1 º, USNM). Trincomalee: Tennamaravadi (1 º, CAS).

## Holotachysphex prosopigastroides Gussakovskij (Fig. 36)

Haplognatha prosopigastroides Gussakovskij, 1952:248, 9. Holotype: 9, Tajikistan:



Figs. 33–35. *Holotachysphex holognathus*, male: 33–forefemoral notch in profile, 34–same, oblique view, 35–same, bottom view.

foothills of Hissar Mts. near Stalinabad, now Dushanbe (ZIN, lost?).—In *Tachysphex*: de Beaumont, 1955:222 (*Haplognatha* synonymized with subgenus *Holotachysphex*).—In *Holotachysphex*: Bohart and Menke, 1976:282 (new combination, listed).

Diagnosis.—At the present time, prosopigastroides cannot be identified with certainty because the unique type was apparently lost (I searched for it in vain during many visits to the Zoological Institute, St. Petersburg, 1963–1980). Gussakovskij's illustration of the head, here redrawn as Fig. 36, shows a clypeus that is unique in the genus, but I suspect that the figure is inaccurate. Possibly Gussakovskij (or his illustrator) made a mistake analogous to my own inaccurate representation of the clypeus in the original description of *schwarzi* Pulawski (1967:409). If so, the dark area on each side of the clypeal process may in fact be a part of the clypeal lobe. Possibly *prosopigastroides* is a synonym of *mochii*, a hypothesis that can only be verified by collecting additional material in Tajikistan or adjacent areas of Afghanistan.

Description (selected from Gussakovskij 1952).—Posterior mandibular margin entire. Clypeal free margin with fingerlike projection (Fig. 36). Scutum coarsely, sparsely punctate. Punctures on terga I and II slightly finer than in *Prosopigastra orientalis* de Beaumont; on tergum I most interspaces smaller than punctures. Length 8.5 mm.

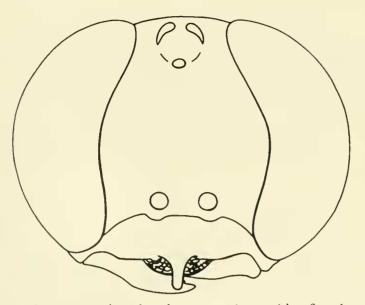


Fig. 36. *Holotachysphex prosopigastroides*: female head in frontal view (redrawn from Gussakovskij 1952).

Gaster black except sternum II largely red. Femoral apex, tibiae, and tarsi ferrugineus except foretibia somewhat darkened mesally.

Geographic distribution.—Known only from type locality in Tajikistan.

Record. – Tadjikistan: Dushanbe (Gussakovskij 1952).

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